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1 **Stable isotopes reveal the effects of maternal rank and infant age on**
2 **weaning dynamics in wild chacma baboons**

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ABSTRACT

15 Maternal strategies reflect the trade-off between offspring needs and maternal ability to invest, a concept
16 described by the evolutionary theory of parent-offspring conflict. In mammals this conflict has often been
17 investigated by studying weaning, the transition from maternal milk consumption to dietary independence. An
18 investigation of individual variation in weaning can provide information on the adaptive significance of
19 maternal strategies in relation to social and biological variables. We analysed nitrogen stable isotopes of hair
20 samples collected from 22 mother-infant dyads in a wild population of chacma baboons (*Papio ursinus*), in
21 conjunction with behavioural data on suckling, to explore the temporal dynamics of weaning, as well as the
22 extent and determinants of individual variation in these dynamics. The weaning pattern suggested by isotope
23 values and behavioural data were congruent. The difference between infant and mother stable nitrogen isotope
24 values decreased faster with age in infants of low-ranking mothers, which suggests a faster progression towards
25 weaning, perhaps due to subordinate females experiencing lower resource availability and so being less able
26 to bear the costs of lactation over prolonged periods. Additionally, within-infant variation in stable nitrogen
27 isotope values showed an increase with age (which was not detectable between infants), potentially
28 highlighting the nutritional costs that weaning imposes on offspring. Our combination of isotope analysis and
29 behavioural data from a wild population provides insight into the evolution of maternal strategies. In particular,
30 it suggests that the quantity of care a mother can provide is affected by her rank, with subordinate females
31 possibly not able to lactate for as long and perhaps benefiting from weaning earlier.

32 **Key words:** Breastfeeding; Maternal strategy; Nitrogen stable isotopes; Chacma baboons; Dominance rank

33
34 Mammalian reproduction involves obligatory maternal care to ensure an offspring's immediate survival and
35 growth, and potentially enhance their future reproductive success and longevity (König and Markl 1987). Yet
36 maternal care entails costs that can impact a female's ability to reproduce in the future (Trivers 1972; 1974).
37 The evolutionary trade-off between investing in current offspring and saving energy for future reproduction
38 generates a conflict: while mothers are expected to adjust the amount of maternal care they provide, weighing
39 up the benefits for current offspring against the costs for future progeny, offspring are expected to prioritize
40 their own fitness and maximise the level of maternal care received (Trivers 1974).

41 In mammals, lactation is considered the most energetically demanding stage of maternal investment,
42 after which mothers usually resume their cycle and reproduce again (Thompson et al. 2012). The process of
43 offspring gradually reducing their reliance on maternal milk to gain nutritional independence is called weaning
44 (Trivers 1974; Martin 1984). Decreased reliance on milk may reflect a progressive quantitative decline in milk
45 consumption, or alternatively a stable milk dependency throughout development associated with a progressive
46 increase in the consumption of solid food (whereby lactation ceases suddenly at the end of the weaning process)
47 (Van Noordwijk, Kuzawa and Van Schaik 2013). Hence, weaning is a change in offspring dependence on their
48 mother as a function of time (Martin 1984), and variation in this reflects variation in the mothers' and
49 offspring's strategies adopted to overcome the parent-offspring conflict (Trivers 1972; Lee 1987; Maestriperi
50 2002). Weaning dynamics directly affect the maternal reproductive trade-off, with earlier weaning leading to
51 shorter inter-birth intervals and higher reproductive rates in mothers, but poorer survival, growth and fitness
52 in the weaned offspring (Trivers 1974; Thompson et al. 2012). Consequently, studying individual variation in
53 the timing of weaning and assessing which ecological, maternal or infant characteristics lead to this variation,
54 is informative for our understanding of demographic processes and the evolution of mother-offspring
55 relationships.

56 Parental investment theory (Trivers 1972) predicts that individuals should care for their current
57 offspring over a longer period of time when they are less likely to reproduce again in the future, or when they
58 need to spread the costs of lactation so they can better afford them on a daily basis. The first case often applies
59 to older females, with the "terminal investment hypothesis" (Williams, 1966) predicting increased care for the
60 last offspring of their reproductive career. In the second case, the "targeted investment hypothesis" (Cameron
61 et al. 2000) suggests that mothers in poor condition who are limited in the daily energy they can invest in care,
62 may compensate by allocating a longer period of care to their offspring. For example, this would be expected
63 within social groups in low-ranking mothers as they are less able to access high-quality resources and so are
64 in worse physical condition (Silk et al. 1981; Arlet et al. 2014). Finally, maternal investment should also be
65 directed towards the offspring sex that will benefit most from it (Trivers and Willard 1973; Reitsema et al.
66 2016; Bădescu et al. 2022). According to the "fragile male hypothesis", sons are physiologically more
67 vulnerable to environmental stress and increased lactation effort may improve their survival chances (Lee and
68 Moss 1986; Wells 2000). Mothers might also obtain inclusive fitness benefits from investing in sons, in species

69 where males generally have the potential for greater reproductive success compared to females (Trivers and
70 Willard 1973; Hewison and Gaillard 1999). Finally, in sexually dimorphic species, male offspring usually need
71 to grow more than females to reach full adult size, and so often receive more maternal care (Trivers and Willard
72 1973; Hewison and Gaillard 1999; Fedigan et al. 2008; Gesquiere et al. 2018).

73 Most studies investigating weaning have been based on life-history data, such as length of lactational
74 anoestrus, and on behavioural data looking at how suckling activity decreases with age, e.g., African elephants
75 (*Loxodonta africana*: Lee and Moss 1986), pinnipeds, ungulates and primates (Lee, Majluf and Gordon 1991),
76 hooded seal (*Cystophora cristata*: Lee 1996), chacma baboons (*Papio ursinus*: Johnson 2003), rhesus
77 macaques (*Macaca mulatta*: Hinde et al. 2009a), African elephants (*Loxodonta africana africana*: Wisniewska
78 et al. 2015), mice (*Mus musculus*: Franks, Champagne and Curley 2015), mountain gorillas (*Gorilla beringei*
79 *beringei*: Eckardt et al. 2016), yellow and olive baboons (*Papio cynocephalus* and *P. anubis*: Gesquiere et al.
80 2018), and Eastern chimpanzees (*Pan troglodytes schweinfurthii*: Lonsdorf et al. 2019). Yet behavioural
81 observations of suckling time and nipple contact may overestimate weaning age (Lonsdorf et al. 2019; Bădescu
82 et al. 2017) because they are unable to distinguish “nutritional nursing” from “comfort nursing”, i.e., oral
83 contact with the nipple without milk transfer (Martin 1984; Borries et al. 2014). It is also possible that comfort
84 nursing increases with age, with nipple contact serving more as pacifier than as a source of nutrition (Martin
85 1984; Borries et al. 2014). Additionally, behavioural data may underestimate weaning age by only reporting
86 diurnal suckling bouts and not accounting for nursing time during the night, when observations are not
87 normally conducted (Reitsema 2012).

88 A more reliable approach to investigate variation in weaning time uses stable isotope signatures
89 (Higgins et al. 1988; Cameron et al. 1998; Fuller et al. 2006; Newsome et al. 2006; Dalerum et al. 2007;
90 Crowley 2012; Reitsema 2012; Reitsema et al. 2016; Bădescu et al. 2017). This method is based on the
91 principle of “you are what you eat”, because the body’s isotope composition reflects its diet over the period of
92 tissue synthesis (Fuller et al. 2006; Reitsema 2012; Oelze et al. 2016). Nitrogen stable isotopes reflect the
93 nitrogen content of amino acids in dietary proteins (DeNiro and Epstein 1981; Bădescu et al. 2017). They are
94 measured using the ratio of ^{15}N to ^{14}N ($\delta^{15}\text{N}$), which reflects trophic position (DeNiro and Epstein 1981;
95 Gannes, O’Brien and del Rio 1997; Bearhop et al. 2004) because, when N is incorporated into tissues, ^{14}N is
96 excreted faster than ^{15}N (Steele and Daniel 1978). $\delta^{15}\text{N}$ values are useful for describing the weaning process

97 since females produce the milk consumed by suckling infants, who thus occupy a higher trophic level than
98 their mothers, with higher $\delta^{15}\text{N}$ values (Fuller et al. 2006; Newsome et al. 2006). In fact, the $\delta^{15}\text{N}$ values in
99 tissues of suckling primate infants are approximately 2-3‰ higher than those of their mothers (Reitsema 2012;
100 Tsutaya and Yoneda 2015). This mother-infant difference is expected to gradually decrease during the weaning
101 process until it disappears entirely as infants stop consuming milk and consume a diet similar to their mother's
102 (Reitsema 2012; Fahy et al. 2014). Stable isotope signatures can be measured in any tissue, but it may be
103 valuable to use hair samples in weaning studies. This is because hair samples provide information over a time
104 period of weeks to months (the time period over which hair is synthesised; Dalerum and Angerbjörn 2005),
105 their collection is minimally invasive, and they are easy to store and metabolically inert, preserving the
106 information indefinitely (Crowley 2012; Oelze 2016).

107 In this study we used stable isotope analysis to investigate variation in weaning age in wild infant
108 chacma baboons (*Papio ursinus*). Chacma baboons are sexually dimorphic primates that live in multimale-
109 multifemale groups, characterised by female philopatry, stable matrilineal hierarchies and promiscuous mating
110 (Fischer et al. 2019). Maternal care in baboons is costly, with lactating females having reduced feeding time
111 and body mass (Barrett, Halliday and Henzi 2006). In chacma baboons there is evidence that females face
112 reproductive trade-offs, for example over the timing of birth which can either maximise offspring survival
113 (current reproduction) or minimize maternal interbirth intervals (future reproduction; Dezeure et al. 2021a). It
114 appears this birth timing trade-off then influences mother-offspring conflict after birth since infants born at
115 times sub-optimal for their own survival throw more tantrums (Dezeure et al. 2021a). Increased maternal
116 investment in baboons has been linked to maternal characteristics and environmental conditions, such as lower
117 maternal rank (Johnson 2006), reduced food availability, or increased competition in larger groups containing
118 more females (Altmann and Alberts 2003).

119 The goals of our study were twofold. First, we aimed to characterize the temporal dynamics of weaning at the
120 population level using stable isotope measures, and then compare these to the dynamics estimated from
121 suckling observations to compare the estimates produced by these two methods, and provide an accurate
122 population-level estimate of weaning age. Second, we aimed to test hypotheses about individual variation in
123 weaning time. We predicted that weaning would occur later in male offspring (who are costlier to raise;

124 Hewison and Gaillard 1999) and in those with older mothers (terminal investment hypothesis; Williams, 1966)
125 or lower-ranking mothers (targeted investment hypothesis; Cameron et al. 2000).

126

METHODS

Study site

127 We collected data in central Namibia, at the Tsaobis Baboon Project (22°23'S, 15°45'E), during three field
128 seasons (May-December 2006, July-December 2018 and April-July 2019). The Tsaobis environment is very
129 arid (mean annual rainfall \pm SD = 192 \pm 143mm) and seasonal, with most rain falling between January and
130 April (Dezeure et al. 2021a), when temperature often exceeds 40°C. The landscape is characterised by two
131 habitats: open rocky desert and riparian woodland patches. The open desert is dominated by small herbs and
132 dwarf bushes, such as *Monechma cleomoides*, *Sesamum capense*, and *Commiphora virgata*. The riparian
133 woodland is dominated by large trees such as *Faidherbia albida*, *Prosopis glandulosa* and *Salvadora persica*,
134 growing along the ephemeral Swakop River (Cowlshaw and Davies 1997). The baboons' diet predominantly
135 consists of flowers, leaves, berries and pods (Cowlshaw 1997). We studied two wild troops of chacma
136 baboons, named L and J (troop sizes: total individuals, adult females, adult males. 2006: L = 32, 9, 7 and J =
137 57, 16, 9; 2018: L = 75, 19, 4 and J = 58, 16, 4; 2019: L = 85, 19, 5 and J = 62, 16, 5). Both troops have been
138 studied since 2005 and are habituated to the presence of researchers at close proximity. All adults and most
139 juveniles are individually identifiable using ear notches and naturally occurring markings (Huchard et al.
140 2010).

141

Field methods

Hair collection

142 We used hair samples collected from 22 mother-infant pairs on October 12th (troop J, $N=9$) and 26th (troop L,
143 $N=5$) 2006, October 9th (troop L, $N=2$) and 16th (troop J, $N=3$) 2018 and May 21st (troop L, $N=3$) 2019. On
144 these dates the troops were undergoing routine capture to collect morphological data and biological samples.
145 Individual baboons were captured at dawn in separate metal cages (c. 2m x 1m x 0.5m) that were baited with
146 corn cobs. Mothers were sedated in the cage at the trapping site by a registered wildlife veterinarian with 100
147 mg/ml of tiletamine–zolazepam (Zolatil™Virbac Australia Ltd, NSW, Australia) at a dose rate of 5 mg/kg

148 administered intramuscularly using a pole syringe. Infants were not anaesthetised and were transported with
149 sleeping mothers in covered cages to a shaded processing area. The anaesthesia lasts 30-45 minutes and so
150 mothers were put on a saline drip to prevent dehydration. Young infants (<6 months old) were usually caught
151 in the same cage as their mother and not anaesthetised but held quietly in a blanket by one of the capture team
152 members within sight of their sleeping mother. After the short period when the mother was processed (~10-15
153 minutes), the infant was immediately placed back with their asleep mother in the release cage. Older infants
154 (> 6 months old) are more independent and often trapped independently from the mother. They were
155 anesthetized using the protocol described above and usually placed in release cages with infants or juveniles
156 that were approximately the same size in order to minimize stress during the waking-up period. In 2006, the
157 processing site was located ~10 minutes away by car from the trapping site and individuals were transported
158 in their cage, usually when asleep, to and from the processing site. In 2018-19, individuals were processed in
159 the field, right by the trapping site. In all cases, the release cages were kept in the shade, close to each other,
160 and covered with blankets, and the mother's recovery monitored closely. Care was taken to avoid placing
161 mother-infant pairs, or young juveniles next to unfamiliar adult males. The entire social group was released
162 together at the trapping site once all individuals were fully awake. Hair samples were collected from the thigh
163 (2006) and subscapular (2018, 2019) areas, using sharp scissors to cut as close to the skin as possible. In order
164 to ensure the presence of enough hair in the anagen phase to measure recent dietary intake and minimise the
165 influence of hair in the telogen phase, we collected bulk of hairs from each individual to allow us to use at
166 least the minimum number of hairs suggested by Mekota et al. 2006.

Behavioural data

167 We also collected behavioural data on suckling events from the same mother-infant dyads. We conducted focal
168 observations of infants which lasted 60 minutes in 2006 (mean focal hours per individual \pm SD=11.8 \pm 1.1,
169 $N=13$ dyads) or 20 minutes in 2018 (12.6 \pm 1.0, $N=4$ dyads) and 2019 (14.8 \pm 1.7, $N=3$ dyads). During focals
170 we recorded whether the infant was suckling, foraging for solid food or engaged in another activity (e.g.
171 locomotion) at five minute intervals. We used these scan observations to calculate, on a monthly basis for each
172 infant, the proportion of feeding scans (suckling and foraging for solid food) in which an infant was observed
173 suckling.

Data on maternal age and rank and infant age

174 Infant ages were easily estimated when birth dates were directly observed. When only the conception date was
175 observed, we added the mean gestation length ($N=190$ days, range: 181-200 days, $SD=5$, $N=13$ pregnancies
176 where both conception and birth were observed) to obtain the birth date. When neither conception nor birth
177 were observed, the birth date was estimated using infant coloration, or, when this was uninformative, the
178 reproductive state of mother in the preceding field season (see Dezeure et al., 2021b for further details on the
179 estimation of birth dates in this population). Among the 22 infants considered in this study, the uncertainty
180 over birth date ranged from 0 to 60 days (median = 10 days). Infants for which the birth date uncertainty was
181 >60 days were not included in this study.

182 Maternal ages were estimated through dental eruption and molar wear patterns recorded in this
183 population during trapping. Briefly, age up to the eruption of the last molar was estimated using Kahumbu and
184 Eley's (1991) eruption schedule. Beyond this age, molar wear rates were estimated from individuals captured
185 at multiple time points and extrapolated across all individuals. These estimates have been validated by
186 comparison of known age differences versus those estimated by molar wear in 19 individuals trapped multiple
187 times over 1-5 years (but not included in the initial estimation of molar wear rates; see Huchard et al. 2009 for
188 further details). Adult dominance ranks in each troop were established from *ad libitum* or focal observations
189 of agonistic and approach-avoidance interactions. These were used to calculate a dominance hierarchy in
190 Matman 1.1.4 (De Vries 1998). Landau's linearity index showed that these hierarchies were linear (2006,
191 troop L: $h=0.95$, $X^2=63.63$, $P<10^{-4}$, troop J: $h=0.67$, $X^2=93.55$, $P<10^{-4}$; 2018, L: $h=0.25$, $X^2=26.11$, $P=0.089$,
192 J: $h=0.38$, $X^2=37.83$, $P=0.016$; 2019, L: $h=0.31$, $X^2=33.26$, $P=0.027$). In order to control for differences in
193 troop size between years and troops, relative rank was calculated as $(N-\text{absolute rank})/(N-1)$, with N the number
194 of adult females in the group in a given year. This measure ranged from 0 to 1, with 0 for the lowest ranking
195 female and 1 for the highest ranking.

196

Ethical note

197 This research adhered with the ASAB/ABS Guidelines for the Use of Animals in Research, the Namibian legal
198 requirements and was carried out with the permission of the Ministry of Environment and Tourism, the
199 Ministry of Land Reform, and the National Commission on Research, Science, and Technology. Our research
200 procedures were evaluated and approved by the Ethics Committee of the University of Roehampton, the Ethics

201 Committee of the Zoological Society of London and the Ministry of Environment and Tourism, Namibia (MET
202 Research / Collecting Permits 1039/2006, RPIV00392018/2019).

203

Hair sample preparation and analysis

204 Hair samples from the 22 mother-infant pairs were prepared for stable isotope analyses at the University of
205 Roehampton. Hairs were washed in deionised water, scraped to remove any lipids, dirt and contaminants, and
206 finally dried in the oven at 60°C for 30 minutes (Robertson et al. 2015; Sheppard et al. 2018). We avoided
207 using chemical treatments to remove free lipids as these can distort carbon and nitrogen isotope ratios (Perkins
208 et al. 2013, Elliot et al. 2014). Each hair was partitioned into 1cm sections, with each section representing
209 approximately one month's growth in chronological order (the section nearest the root being the most recent;
210 hair growth rates based on primate hair growth rates reported by Oelze 2016). Our analysis required the
211 comparison of isotope values obtained from mother-infant pairs from the same time period. In each pair we
212 obtained 3 to 5 segments (mean=4.09, $N=22$) from each individual. Each segment was homogenised using a
213 scalpel and 0.7mg±0.1mg of this sample was weighed out and sealed into tin capsules (Elemental
214 Microanalysis).

215 Previous isotopic analyses of weaning have used both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ($^{12}\text{C}/^{13}\text{C}$) isotope ratios (Reitsema
216 2012; Beaumont et al. 2015). However, $\delta^{13}\text{C}$ is more sensitive to habitat changes, gives less information about
217 trophic discrimination and decreases to maternal levels more quickly than $\delta^{15}\text{N}$ (Fuller et al. 2006; Reitsema
218 2012). In our study, the difference between infant-mother $\delta^{13}\text{C}$ values decreased rapidly with infant age and so
219 was not informative about variation in weaning age (supplementary materials: Figure S1). This is likely to be
220 because, as suggested by Fuller et al. (2006), the drop of infants $\delta^{13}\text{C}$ values indicates the introduction of solid
221 food in the diet rather than the duration of breast milk consumption, and infants start consuming solid food
222 while still relying on breast milk.

223 Samples were run on a Europa Scientific 2020 isotope ratio mass spectrometer linked to a Thermoquest
224 EA1110 elemental analyser running in continuous flow mode at Elementx Ltd (Gunnislake, UK). Isotope ratios
225 were expressed as δ values, using parts per million (‰) (O'Brien and Wooler 2007; Crowley 2012), according
226 to the equation:

227

$$\delta X = (R_{\text{sample}}/R_{\text{standard}}) - 1 \times 1000$$

228 where X represents ^{15}N and R the ratio of heavy to light isotopes ($^{15}\text{N}/^{14}\text{N}$). International reference materials
229 (IAEA, Vienna) were also analysed within each run for calibration, with $\delta^{15}\text{N}$ samples values scaled to AIR.
230 In order to assess the quality of these isotope data we checked that the C:N ratios ranged between 3.00 and
231 3.80 (O'Connell et al. 1999). The mean C:N for our hair samples was 3.43 (SD = 0.14, range = 3.11-3.79).

232

Statistical Analysis

1. Population-level weaning dynamics

233 We analysed population-level weaning trends using $\delta^{15}\text{N}$ stable isotope values following Reitsema et al.'s
234 (2016) method to detect breastfeeding by comparing maternal and infant stable isotope values from the same
235 time period. To do this we compared each infant's monthly $\delta^{15}\text{N}$ value with their mother's mean $\delta^{15}\text{N}$ value
236 ($\Delta^{15}\text{N}$) to control for variation in isotope values caused by changes in maternal diet (Reitsema et al. 2016). This
237 comparison process involved four steps: (1) In each mother-infant pair, we calculated the mean $\delta^{15}\text{N}$ value for
238 each mother across all hair sections. This mean value was calculated across all monthly infant values, to control
239 for short-term fluctuations in the mother's diet during this period and provide a value representing baseline for
240 each female. (2) We then subtracted this mean value from each infant's monthly $\delta^{15}\text{N}$ value to produce monthly
241 $\Delta^{15}\text{N}$ values. (3) We then calculated the mean $\Delta^{15}\text{N}$ values across infants for each monthly infant age. Each
242 monthly value was based on 3-12 infants (median 7, $N= 12$ months), with each infant contributing to 3-5
243 months (median = 4). We excluded values from ≤ 5 months and ≥ 18 months of age, as $N = 1$ for these age
244 ranges. (4) Finally, we plotted the mean $\Delta^{15}\text{N}$ values against infant age to characterise the weaning process in
245 this population.

246 In addition, we compared the trend described by $\Delta^{15}\text{N}$ values with the trend described by our suckling
247 observations. Here, we calculated the mean proportion of feeding scans (suckling and foraging for solid food)
248 in which an infant was observed suckling for each monthly infant age. We then compared the distribution of
249 these proportions across monthly infant ages with the distribution of our $\Delta^{15}\text{N}$ values using Kolmogorov-
250 Smirnov tests.

251 Finally, we estimated weaning ages for each individual by comparing the resulting $\Delta^{15}\text{N}$ values with
252 the range of variation of $\delta^{15}\text{N}$ for mothers in this population, calculated here as the standard deviation of the

253 mean maternal $\delta^{15}\text{N}$ (0.805). An infant was considered weaned when its $\Delta^{15}\text{N}$ values were equal or below to
254 the standard deviation (for examples of these estimations, see supplementary materials: Figure S2).

255

2. *Individual variation in weaning*

256 We tested our predictions about the influence of offspring sex, maternal rank and maternal age on weaning by
257 running two complementary models with normal error structure: (1) a linear model (LM) with weaning age
258 estimates as response variable, and (2) a linear mixed model (LMM) with $\Delta^{15}\text{N}$ values as response variable.
259 The first model provided a direct analysis of weaning age, but each infant only contributed a single point, and
260 the sample was limited only to those infants for which we were able to estimate a weaning age ($N= 12$). The
261 second model assessed progression towards weaning by measuring changes in $\Delta^{15}\text{N}$ values in relation to infant
262 age. In this model, each infant contributed multiple points and the sample included all infants ($N= 90$ measures
263 from 22 infants). Offspring sex, maternal rank and maternal age were included as fixed effects in both models.
264 We included infant ID as random intercepts in our model of $\Delta^{15}\text{N}$ values to control for repeated measures
265 (Mundry and Oelze 2016), while year and troop were included as fixed effects in both models to control for
266 between troop and year effects. We also considered a possible quadratic effect of maternal age; females' IBIs
267 are longer for both youngest and oldest individuals (Gesquiere et al. 2018), thus a similar effect could be found
268 in terms of the length of the lactation period. To do so, we compared the models' performance using AICc
269 values in the MuMIn package (Barton 2020). Models including a quadratic age effect always performed worse
270 (higher AICc values - supplementary materials: Table S1) than those including a simple age effect, so we did
271 not present these models here.

272 As infants get older and closer to being fully weaned, they reduce their reliance on maternal milk, and
273 so their $\Delta^{15}\text{N}$ values are expected to decrease (Bădescu et al. 2017); thus we also included infant age in our
274 model of $\Delta^{15}\text{N}$ values to control for this. However, in our dataset, age varied both within and between
275 individuals as each infant was associated with more than one age value (corresponding to the different 1cm-
276 sections of hair). This raised the possibility that the effect of age could be different within and between
277 individuals. We therefore followed Van de Pol and Wright's (2009) within-subject centring technique. Here,
278 the between-individual effect was estimated by fitting each infant's mean age across all of its $\Delta^{15}\text{N}$ values,

279 whilst the within-individual effect was estimated by fitting the difference from each infant's mean age for each
280 $\Delta^{15}\text{N}$ value.

281 In our model of $\Delta^{15}\text{N}$ values we fitted an interaction between each of the age variables, (i) between-
282 infant age and (ii) within-infant age effect, and offspring sex, maternal rank and age to test our prediction that
283 an infant's weaning is influenced by its own and its mother's characteristics. When these did not have a
284 significant effect, we dropped them from our final model to allow us to test the significance of the main effects
285 in these nonsignificant interactions (Engqvist 2005).

286 Since our first model predicting weaning age was fitted using a small data set ($N = 13$), there was potential
287 for this to be overparametrized. Therefore, we ran three additional univariate models using maternal rank,
288 maternal age and offspring sex separately to predict plotting weaning age estimates, with year and troop as
289 random effects. To check for multicollinearity, we calculated the variance inflation factor (VIF) for each
290 predictor in each full model using the 'vif' function in the 'car' package (Fox and Weisberg 2018). All VIFs
291 were < 3 across all our final models. We checked that each model met the assumptions that the residuals were
292 normally distributed and had homogeneous variance and that explanatory variables were independent.

293 We conducted all of our analyses using the program R version 3.6.1 (R Core Team, 2019), fitting the LM
294 using the "stats" package (R Core Team, 2019), fitting the LMMs using the "lme4" package (Bates et al.,
295 2015) and calculating models' r^2 values using the "MuMIn" package (Barton 2020).

296

RESULTS

1. Population-weaning dynamics

297 The mean values of $\Delta^{15}\text{N}$ in relation to infant age are shown in Figure 1a. Mean values of $\Delta^{15}\text{N}$ stayed relatively
298 low from month 8, generally decreasing to month 17 describing the gradual process of weaning. Comparing
299 the behavioural and isotopic measures of weaning, the proportion of feeding scans that infants spent suckling
300 was relatively low between months 11 and 13 (mean \pm SD: 0.0434 ± 0.0256 , Figure 1b), but, in months 14 to
301 16 when $\Delta^{15}\text{N}$ values were at their lowest (Figure 1a), the mean time spent suckling was relatively high (mean
302 \pm SD: 0.227 ± 0.0531) before decreasing again at month 17. Supporting these observations, the $\Delta^{15}\text{N}$
303 distribution was significantly different from the distribution of the proportion of suckling time (Kolmogorov-
304 Smirnov test: $D=1.00$, $P<10^{-4}$).

Estimation of weaning ages

305 It was only possible to estimate the weaning age for 13 out of 22 infants. For the remaining 9 infants, our hair
306 samples did not capture the time period where $\Delta^{15}\text{N}$ values fell below the level of the between-mother variation
307 (SD: $\delta^{15}\text{N}=0.805$). For the 13 infants where this time period was captured, the mean (\pm SD) weaning age was
308 estimated at 12.3 (\pm 2.5) months.

309 In the 9 infants where it was not possible to estimate a weaning age, 7 had $\Delta^{15}\text{N}$ values that remained
310 greater than the level of between-mother variation, suggesting they had not weaned when we collected their
311 hair samples. The remaining 2 were old enough to have started feeding away from the mother and closer to
312 the father (Huchard et al. 2013), thus we suggest they had weaned before the time period our hair samples
313 captured (supplementary materials, Figure S3). To confirm these assumptions, we performed Mann-Whitney
314 tests, comparing the age distribution (i.e. the ages from each hair sample) of these two groups with the age
315 distribution for the group for which we were able to estimate a weaning age. The infants who we suspected
316 were not yet weaned were younger (mean age \pm SD: 8.29 \pm 2.14 months) than the infants for whom we
317 estimated a weaning age (mean age \pm SD: 12.57 \pm 2.07 months; $W=12.5$, $P=0.0088$, $N=19$; Fig. S3). The
318 infants who we suspected had weaned before our sampling period appeared older (mean age \pm SD: 16 \pm 2.73
319 months) than the infants for whom we estimated a weaning age, although the statistical comparison only
320 approached significance ($W=63$, $P=0.051$, $N=18$; Fig. S3). Additionally, we confirmed that infants who we
321 suspected were not weaned were younger than the infants who we suspected were already weaned ($W=88$,
322 $P=0.00051$, $N=19$; Fig. S3).

2. Determinants of individual variation in weaning

323 Our weaning age estimates varied between troop and year, but were not predicted by maternal age, rank or
324 offspring sex (Table 1). This is in line with the results of the additional univariate analyses that we ran in order
325 to check that the results of our main model were not produced by overparameterisation (supplementary
326 materials, Table S2). Our analysis of $\Delta^{15}\text{N}$ values indicated an interactive effect of rank and between-infant
327 age (Table 1), such that $\Delta^{15}\text{N}$ values decreased with age for infants of lower ranking mothers whereas they
328 were relatively stable for infants of higher-ranking mothers (Figure 2). Additionally, the $\Delta^{15}\text{N}$ values increased
329 with within-infant age effect (Figure 3) potentially indicating an increase in nutritional stress, which we explore
330 further below. Neither maternal age, offspring sex, troop nor year predicted $\Delta^{15}\text{N}$ values (Table 1). In order to

331 account for the fact that the within-infant age effect may vary with age, we also ran a model including random
332 within-individual age effect slopes for each individual, which confirms our results (supplementary materials,
333 Table S3). The results for the non-significant interactions in the $\Delta^{15}\text{N}$ model are reported in the supplementary
334 materials (Table S4).

335

DISCUSSION

336 We used stable isotope analysis to estimate weaning ages in wild chacma baboons and to test hypotheses of
337 parental investment theory about individual variation in weaning. Our data estimate that weaning occurs in
338 this population at a mean \pm S.D. age of 12.3 ± 2.5 months. Contrary to our expectation, our findings suggest
339 that the offspring of lower-ranking mothers progress towards weaning more quickly than those of higher-
340 ranking mothers (between-infant effect). We also found that, as an infant gets older, it exhibits higher $\Delta^{15}\text{N}$
341 values, possibly an indication of nutritional stress (within-infant effect; Deschner et al. 2012; Bădescu et al.
342 2017). We did not find any support for the prediction that the offspring of older mothers wean later. Our study
343 indicates the importance of a parent's social environment in the weaning process, and how this may impose
344 nutritional costs on offspring. It also highlights the use of stable isotopes in measuring variation in this weaning
345 process, especially in wild populations.

346

Individual variation in weaning

347 Our results highlight how social environment plays an important role in weaning, with the offspring
348 of lower-ranking mothers moving towards nutritional independence faster than the offspring of high-ranking
349 mothers (rather than more slowly as we predicted). This pattern was not observed in our analysis of weaning
350 age, possibly because the weaning age model had much lower statistical power (both a smaller sample of
351 infants and fewer data points per infant). Dominance enhances female reproductive success, with advantages
352 such as priority access to food and offspring survival (Smuts and Nicolson 1989; Johnson 2003; Arlet et al.
353 2014), but the evidence for how rank affects weaning differs between studies (e.g. Gomendio 1990; Eckardt
354 et al. 2016; Gesquiere et al. 2018; Lonsdorf et al. 2019), which presumably reflects the influence of other
355 variables. In particular, ecological conditions can influence female weaning decisions (Lee et al. 1991;
356 Altmann and Alberts 2003; Gesquiere et al. 2018), impacting maternal physiological state and hence affecting

357 maternal strategy. Lee, Majluf and Gordon's (1991) comparative study across pinnipeds, ungulates and
358 primates showed that, when food availability is more restricted, female mammals with relatively low
359 nutritional status adopt an early weaning strategy, limiting how long they need to lactate. In contrast, late
360 weaning is associated with a more abundant food availability, allowing females to sustain the costs of
361 investment over a longer time period (Lee et al. 1991). Our study population lives in relatively harsh semi-
362 desert environment (Cowlshaw and Davies 1997) and it appears that, in these conditions, lower-ranking
363 mothers were less able to cope with the costs of lactation, and thus progressed towards weaning their infants
364 earlier than more dominant females. Low-ranking mothers could alternatively, or in addition, have reduced the
365 amount of maternal investment per unit of time they provide (Smuts and Nicolson 1989; Rachlow and Bowyer
366 1994). A lower amount of maternal care directly affects the maternal reproductive trade-off, and a faster
367 weaning process has often been associated with shorter inter-birth intervals (IBIs) and lower offspring survival
368 (Trivers 1974; Thompson et al. 2012). However, in this population lower-ranking females have longer IBIs
369 than more dominant females (Dezeure et al. 2021a), despite the faster progression towards weaning we
370 observed here. This shows the added benefit of isotopic data, suggesting that inferences on weaning age based
371 on the length of lactational anoestrus (e.g. Johnson 2003; Gesquiere et al. 2018) may be misleading, because
372 subordinate females may not be able to finance prolonged lactations and may subsequently need a longer time
373 to replenish their energetic stores. Moreover, offspring survival, which is more important than IBI in
374 influencing maternal lifetime reproductive success (Weibel et al. 2020), is not influenced by maternal rank in
375 the Tsaobis population (Dezeure et al. 2021a), which suggests that rank influences maternal weaning strategy,
376 but not necessarily female reproductive success. Another possible explanation is that low-ranking females
377 accelerated weaning as a counterstrategy to infanticide from males (Colmenares and Gomendio 1988; Beehner
378 and Bergman 2008), though it's not clearly established that subordinate females are more vulnerable than
379 dominant ones in baboons. Male hierarchy instability may often increase infanticide risk (Baniel et al. 2018,
380 Beehner et al. 2005), and our population was more stable in 2006 compared to 2018 and 2019, but our analysis
381 did not show any year effect on weaning age. However, our sample only covers three different years and
382 females may also engage in other strategies to protect their offspring from infanticide. For example, lactating
383 female baboons can maintain close associations with males to gain protection for their infant (Palombit,

384 Seyfarth and Cheney 1997; Weingrill 2000), and this behaviour may be particularly important for subordinate
385 females with fewer social connections and in case of male takeovers (Beehner and Bergman 2008).

386 Our study also shows a within-infant increase in $\Delta^{15}\text{N}$ values with older age, which might be the result
387 of greater nutritional stress rather than higher trophic position (Crowley 2012; Bădescu et al. 2017). Analysis
388 of stable isotope signatures in multiple taxa has shown that $\delta^{15}\text{N}$ values are elevated under conditions of food
389 deprivation (e.g. low protein diet, reduced food intake, poor environmental or physical conditions; McCue and
390 Pollock 2008) and a recent study on hair samples showed for the first time isotopic evidence for nutritional
391 stress in a free-ranging primate species (Oelze et al. 2020). When individuals experience a negative nitrogen
392 balance (i.e. they are nutritionally stressed because they do not obtain sufficient nitrogen to meet metabolic
393 requirements), they will start to catabolize their own tissues to synthesise the protein needed for survival,
394 reincorporating liberated amino acids, enriched in ^{15}N compared to dietary ones, and thus causing an increase
395 in $\delta^{15}\text{N}$ values (McCue and Pollock 2008; Deschner et al. 2012; Neuberger et al. 2013). Fuller et al. (2006)
396 studied weaning by using stable isotope signatures from pairs of breastfeeding women and their nursing
397 children and suggested that $\delta^{15}\text{N}$ values may be influenced not only by diet but also by nitrogen balance. This
398 matches the established principle that the switch from maternal milk to solid food is nutritionally stressful
399 because solid food is (i) per unit more difficult to digest and less nutritious compared to maternal milk, which
400 contains approximately 16mg/ml protein (Buss 1968), (ii) it is higher in nitrogen content compared to maternal
401 plant-based food (Reitsema 2012), and (iii) more difficult to find and exploit, since infants need to learn
402 foraging skills and compete with the others for food resources (Rhine et al. 1985; Maestriperi 1995). In fact,
403 the transition from exclusive reliance on milk to reliance on solid food may cause infants to be nutritionally
404 stressed, although this has rarely been explored (Franks, Champagne and Curley 2015). The high $\delta^{15}\text{N}$ values
405 caused by nutritional stress is indicated by a relatively low dietary nitrogen content (%N), whereas infants with
406 the high $\delta^{15}\text{N}$ values caused by milk consumption should have higher %N (Bădescu et al. 2017). Urea and
407 faeces' %N values have been found to reflect dietary %N values (Deschner et al. 2012; Bădescu et al. 2017).
408 Petzke et al. (2005) examined the content of human hair and suggested that the amount of hair ^{15}N may
409 similarly reflect the dietary nitrogen content, but the link between hair and dietary %N values is less clear.
410 Establishing such a link would allow studies using stable isotopes analysis of hair samples to investigate the
411 physiological implications of weaning on offspring.

412 While we expected sons to wean later than daughters, as recently found in chimpanzees (Bădescu et
413 al. 2022), we did not find any evidence of sex-bias investment in this study. Such a negative result may reflect
414 the limitations of our sample size to detect small effect sizes. Another possible explanation is that that male
415 and female infant baboon energetic and nutritional needs are comparable since they have similar body sizes
416 with sexual dimorphism appearing once juveniles are nutritionally independent.. Finally, empirical evidence
417 for sex biases in maternal investment has been hard to gather in wild primate populations, often producing
418 mixed and inconsistent results, and it remains difficult to find general patterns fitting with theoretical
419 expectations (Lee 1987; Brown 2001; Hinde 2009b).

420 Lastly, maternal age did not predict offspring weaning, contrary to our expectation that older females
421 would wean their offspring later. The lack of support for this prediction may be because it is generated by the
422 “terminal investment hypothesis” that females invest more care in their final offspring (Williams, 1966), but
423 most mothers in our data were still likely to reproduce in the future. Indeed, female baboons have a median
424 lifespan of 18.5 years (Tung et al. 2016 - maximum observed lifespan of 26.7 years), while in our sample the
425 median maternal age \pm SD was of 14 ± 4.03 years, with only two females older than 18 years and so potentially
426 near the end of their lives.

427 In conclusion, in order to improve our understanding of weaning and weaning-induced nutritional
428 stress, future studies should determine the hair growth rate in baboons and possibly further investigate the
429 correlation between nitrogen hair content and the dietary one.

430

Population-level weaning dynamics

431 Our isotope data estimates a mean \pm SD weaning age in this population of 12.3 ± 2.5 months ($N=13$). This is
432 in line with anecdotal reports from this population that infants older than 1-year old do not necessarily die
433 following their mother’s death, as we would expect for infants still reliant on their mother’s milk for nutrition
434 (E. Huchard, pers. obs.). This weaning age estimate coincides with the marked drop in suckling we observed
435 in offspring aged 11 to 13 months (Figure 1b). However, these behavioural data suggest an abrupt end to milk
436 consumption between 10 and 11 months old, whilst the nitrogen isotope data indicate a more gradual transition
437 (Figure 1a). This gradual process was probably obscured in the behavioural data by a reduction in milk supply
438 before weaning (meaning infants received less milk per unit time of suckling), up to the point where infants

439 needed to forage autonomously to meet their nutritional requirements and mothers may have actively
440 discouraged suckling producing the steep drop in suckling rates at 10 to 11 months. Moreover, data on tantrum
441 behaviour in this population supports our assumption that mothers may be actively preventing their offspring
442 from suckling in this period in order to complete the weaning process (Dezezeure et al. 2021a). In contrast, the
443 increased time spent suckling after month 13 most likely reflects comfort nursing: as weaning infants
444 experience food deprivation and hunger, they start to suckle again but without gaining milk. Indeed, it has been
445 suggested that infants try to cope with the pressure of the nutritional stress that weaning causes by increasing
446 nipple contact post-weaning, even if mothers have stopped producing milk (Hinde et al. 2009a; Bădescu et al.
447 2017; Bădescu et al. 2022).

448 Previous studies tend to analyse weaning by using either behavioural data, e.g., chacma baboons
449 (Johnson 2003), house mice (*Mus musculus*: Franks, Champagne and Curley 2015), and Eastern chimpanzees
450 (Lonsdorf et al. 2019), or isotopic data, e.g, northern fur seals and California sea lions (*Callorhinus ursinus*
451 and *Zalophus californianus*: Newsome et al. 2006), Francois' leaf monkey (*Trachypithecus francoisi*:
452 Reitsema 2012) and rhesus macaques (Reitsema et al. 2016), most of which were also performed on captive
453 populations with an abundant food supply. Although some studies have attempted to correlate measures of
454 time spent suckling with estimates of infant reliance on maternal milk (see the review by Cameron 1998) and
455 with isotopic methods (*Eumetopias jubatus*: Higgins et al. 1988; *Equus caballus*: Cameron et al. 1999), the
456 approach that we have adopted here builds on literature combining isotopic and behavioural data to study
457 maternal strategies (e.g. Cameron et al. 1999; Bădescu et al. 2016; Bădescu et al. 2017; Reitsema et al. 2020;
458 Bădescu et al. 2022), and indicates how these two types of data can be combined in wild populations to provide
459 a more complete picture of the weaning process.

460 Our weaning age estimate of 12.3 ± 2.5 months in our chacma baboon population is in line with other
461 baboon populations. Analyses of postpartum amenorrhea periods suggested that lactation lasted 10.4 ± 2.8
462 months in the yellow baboons of Amboseli, Kenya (*Papio cynocephalus*: Gesquiere et al. 2018), and $13.1 \pm$
463 0.6 months in the olive baboons of Gilgil, Kenya (*P. anubis*: Smuts and Nicolson 1989). Similarly,
464 observations of nipple contact time in olive baboons at the Gombe Stream National Park, Tanzania, suggested
465 weaning ages between 12-18 months (Nash 1978). Nevertheless, different environmental conditions can be a
466 source of variation in the weaning period (Lycett et al. 1998). For example, in chacma baboons who lived in

467 the Drakensberg Mountains, South Africa, where environmental conditions are relatively harsh, offspring
468 spent more time on the nipple and started weaning around 7 months later compared to several East African
469 baboon populations in more benign environments (Lycett et al. 1998). The semi-desert environment at Tsaobis
470 is also relatively harsh, but our weaning estimate is closer to those reported for East Africa than for South
471 Africa. As we found that low-ranked mothers-offspring pairs progressed towards weaning earlier, this may
472 suggest that the costs of harsh conditions disproportionately affect low-ranked females rather than all
473 individuals in the population. However, it is important to take into account methodological variations when
474 making such comparisons. In particular, we know from this study that nipple contact may continue for some
475 months after the completion of weaning, so using suckling behaviour to determine weaning is likely to lead to
476 substantial overestimates. In addition, comfort nursing may be more frequent in harsh environments where
477 weanlings are more nutritionally stressed, and mothers in such environments may also resume cycling more
478 slowly if it takes them more time to recover their condition. Altogether, these complexities make it hard to
479 compare across studies when weaning estimates are based solely on behavioural or life-history measures.

480

CONCLUSION

481 We used stable isotope values to measure variation in weaning in chacma baboon infants and to test hypotheses
482 from parental investment theory. Our results suggest that the offspring of lower-ranking mothers move towards
483 nutritional independence faster than the offspring of higher-ranked mothers, potentially due to differences in
484 subordinate and dominant females' ability to sustain the costs of lactation. Our results also demonstrate the
485 use of isotopic measures in reliably inferring weaning dynamics and age and how they can be used in parallel
486 with behavioural data on suckling frequency from the same individuals. The weaning process is a key period
487 for mammalian offspring development and our study highlights how, in highly social species such as baboons,
488 this process can be influenced by a mother's social position.

489

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500

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TABLE

740 **Table 1**

741 Results of our models predicting estimated weaning age ($N=13$ infants) and $\Delta^{15}\text{N}$ values ($N=90$ samples from
742 22 infants for each measure).

<i>Response variable</i>	<i>Explanatory variable</i>	<i>Estimate</i>	<i>standard error</i>	<i>degree of freedom</i>	<i>T value</i>	<i>P-value</i>
WEANING AGE R ² : 0.918	Intercept	8.102	1.989			
	Maternal age	0.076	0.084	-	0.905	0.40033
	Rank	-0.322	1.048	-	-0.308	0.769
	Offspring sex: Male ^a	0.972	1.040	-	0.935	0.386
	Troop: L ^b	5.032	0.936	-	5.374	0.002
	Year: 2018 ^c	2.668	0.807	-	3.308	0.016
$\Delta^{15}\text{N}$ R ² c: 0.859	Year: 2019 ^c	0.172	1.195	-	0.144	0.890
	Intercept	5.870	1.622			
	Maternal age	0.036	0.043	12.917	0.835	0.419
	Rank	-6.997	3.056	12.959		
	Offspring sex: Male ^a	-0.312	0.346	13.028	-0.902	0.384
	Troop: L ^b	0.597	0.304	12.963	1.967	0.071
	Year: 2018 ^c	-0.088	0.494	12.783	-0.178	0.862
	Year: 2019 ^c	0.369	0.530	12.918	0.696	0.499
	Between-infant age effect	-0.440	0.143	12.972		
	Within-infant age effect	0.196	0.030	66.898	6.635	<0.001
Rank x Between-infant age effect	0.618	0.254	12.922	2.435	0.030	

743 Reference category = ^aFemale; ^bJ; ^c2006

744 R²c is the conditional r² value (Nakagawa et al. 2017). Significant effects are marked in bold. The non-
745 significant interactions were removed from the final models (Engqvist 2005) and are reported in the
746 supplementary material (Table S3).

FIGURE LEGENDS

747 **Fig. 1** Variation with age in (a) the mean difference between infant and mother $\delta^{15}\text{N}$ ($\Delta^{15}\text{N}$) and (b) the mean
748 proportion of feeding scans in which infants were observed suckling. Standard errors are represented by a
749 coloured area around the line. The numbers near each dot indicate the number of individuals contributing to
750 each mean and standard error.

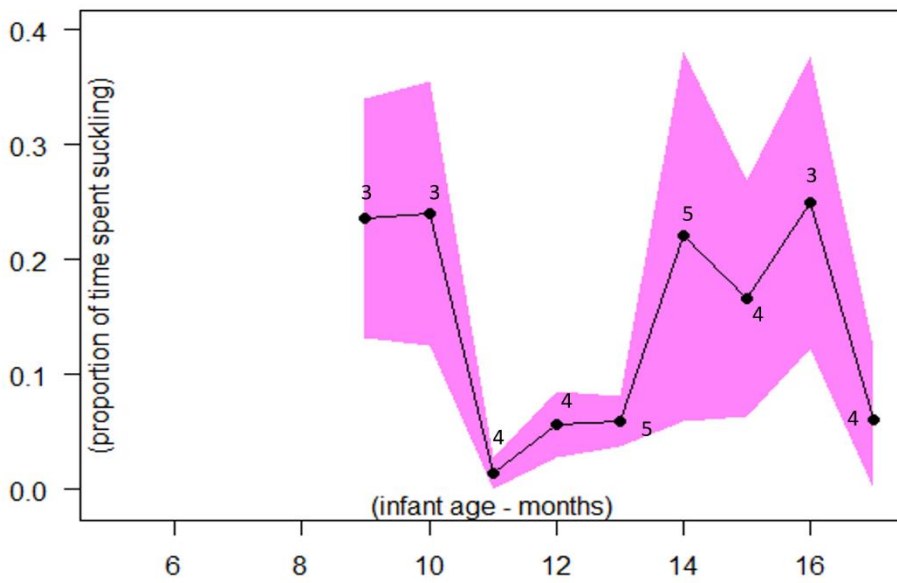
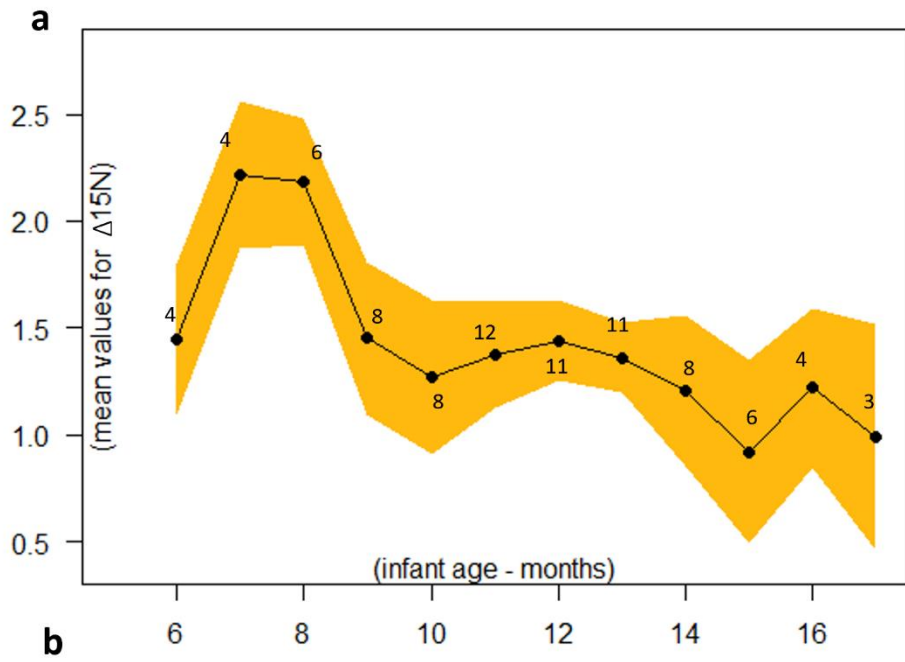
751 **Fig. 2** The interactive effect of maternal rank and between-infant differences in age on $\Delta^{15}\text{N}$ values. The dots
752 show infants with mothers whose rank is below (blue) or above (red) the median rank (0.667). The lines are
753 the predictions of our model for the 25th (rank = 0.38, more subordinate mothers, red line) and 75th (rank =
754 0.80, more dominant mothers, blue line) percentile in our maternal rank data. In these predictions the within-
755 age effect and maternal age are set to their mean, sex to female, troop to L and year to 2006. The shaded areas
756 show the standard error around these predictions.

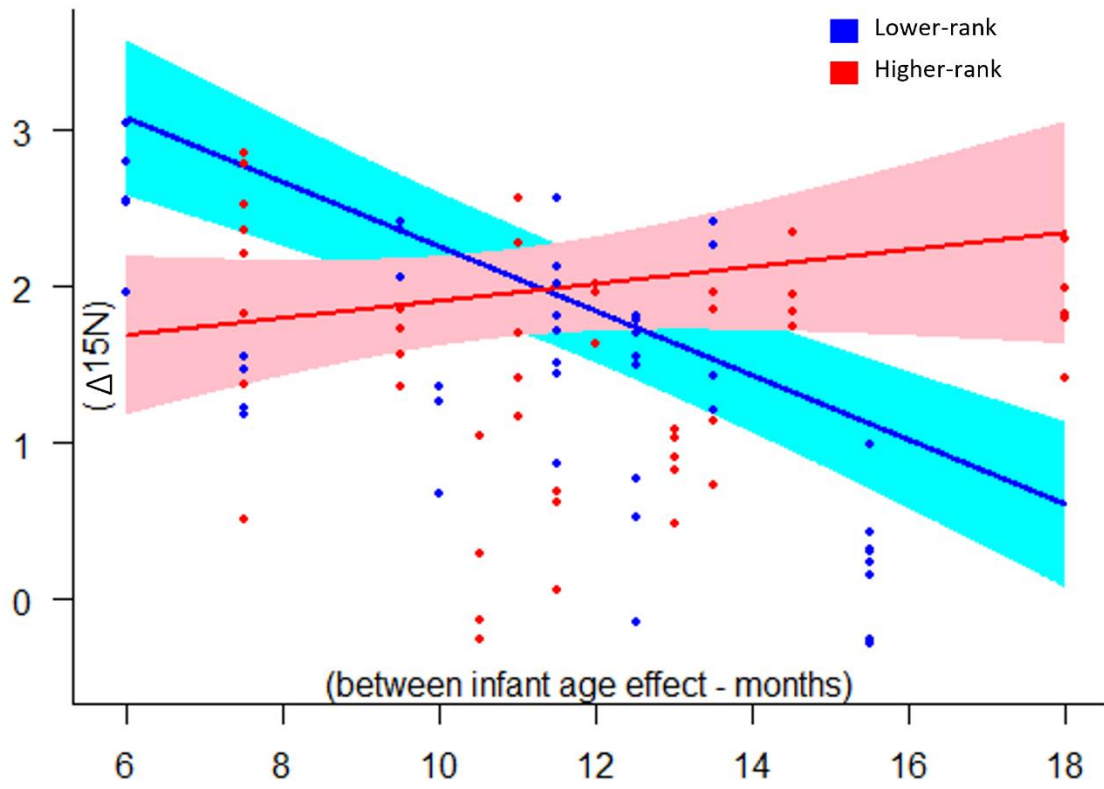
757 **Fig. 3** The within-infant age effect on $\Delta^{15}\text{N}$ values. The line is the effect predicted by our model with all other
758 continuous variables set to their mean, sex set to female, troop to L and year to 2006. The shaded area depicts
759 the standard error around these predictions. In this figure zero represents each infant's mean sampling age,
760 with positive values representing hair sections grown at ages older than the mean, and negative values
761 representing hair sections grown at ages younger than the mean.

FIGURES

762 Fig. 1

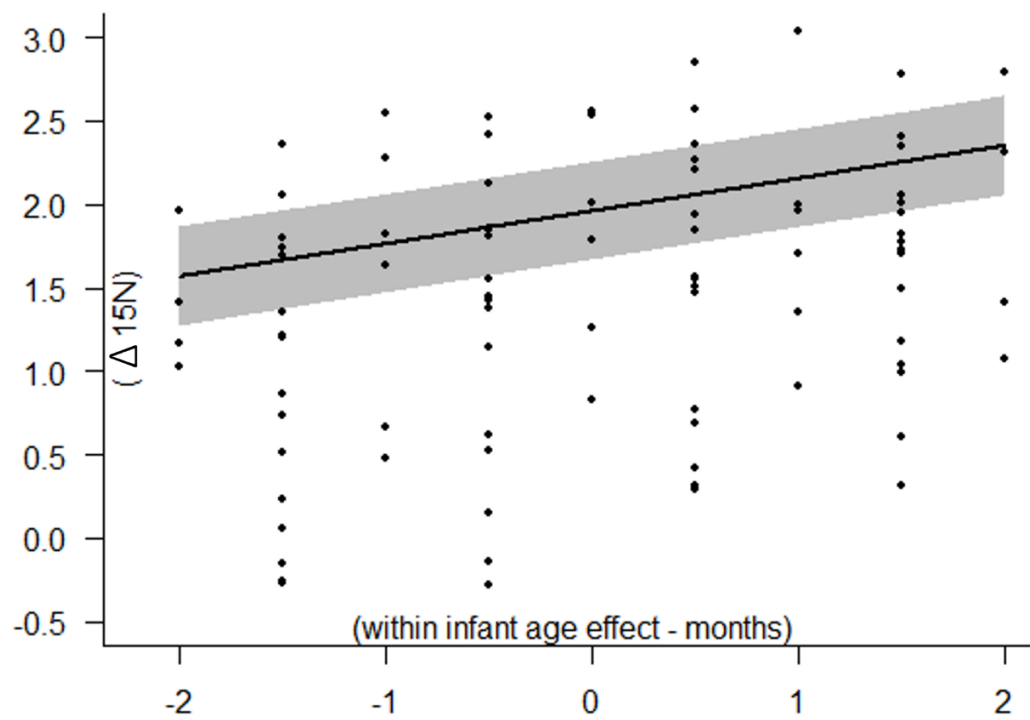
763





765 **Fig. 3**

766



SUPPLEMENTARY MATERIALS

767 **Table S1.** AICc values of the full models predicting weaning age and $\Delta^{15}\text{N}$ including either linear maternal
768 age effect or quadratic (and a linear) maternal age as fixed effects.

Response variable	AIC_c of the model including maternal age	AIC_c of the model including the quadratic effect of maternal age
Weaning age	88.9	125.8
$\Delta^{15}\text{N}$	144.6	155.0

769 **Table S2.** Results of the models predicting estimated weaning ages ($N=13$ infants). Troop and year are
 770 random effects in all models.

<i>Response variable</i>	<i>Explanatory variable</i>	<i>Estimate</i>	<i>standard error</i>	<i>degree of freedom</i>	<i>T value</i>	<i>P-value</i>
WEANING AGE	Intercept	11.74	2.489			
	Maternal rank	0.094	0.065	-	1.448	0.190
WEANING AGE	Intercept	12.77	2.329			
	Maternal Rank	0.282	1.019	-	0.277	0.789
WEANING AGE	Intercept	13.03	2.485			
	Offspring sex: Male ^a	-0.219	1.393	-	-0.158	0.878

771 Reference category = ^aFemale

772 **Table S3.** Results of the model including a random slope for the within-age effect predicting $\Delta^{15}\text{N}$ values
 773 ($N=90$ samples from 22 infants for each measure).

<i>Response variable</i>	<i>Explanatory variable</i>	<i>Estimate</i>	<i>standard error</i>	<i>degree of freedom</i>	<i>T value</i>	<i>P-value</i>
$\Delta^{15}\text{N}$ $R^2c: 0.897$	Intercept	6.123	1.412			
	Maternal age	0.038	0.037	12.737	1.019	0.327
	Rank	-7.672	2.642	12.903		
	Offspring sex: Male ^a	-0.418	0.3001	13.209	-1.392	0.187
	Troop: L ^b	0.601	0.262	12.868	2.291	0.0395
	Year: 2018 ^c	-0.173	0.423	12.183	-0.410	0.689
	Year: 2019 ^c	0.248	0.458	12.831	0.541	0.598
	Between-infant age effect	-0.443	0.124	12.934		
	Within-infant age effect	0.206	0.039	20.217	5.269	<0.001
	Rank x Between-infant age effect	0.655	0.219	12.792	2.990	0.0106

774 Reference category = ^aFemale; ^bJ; ^c2006

775 R^2c is the conditional r^2 value. Significant effects are marked in bold.

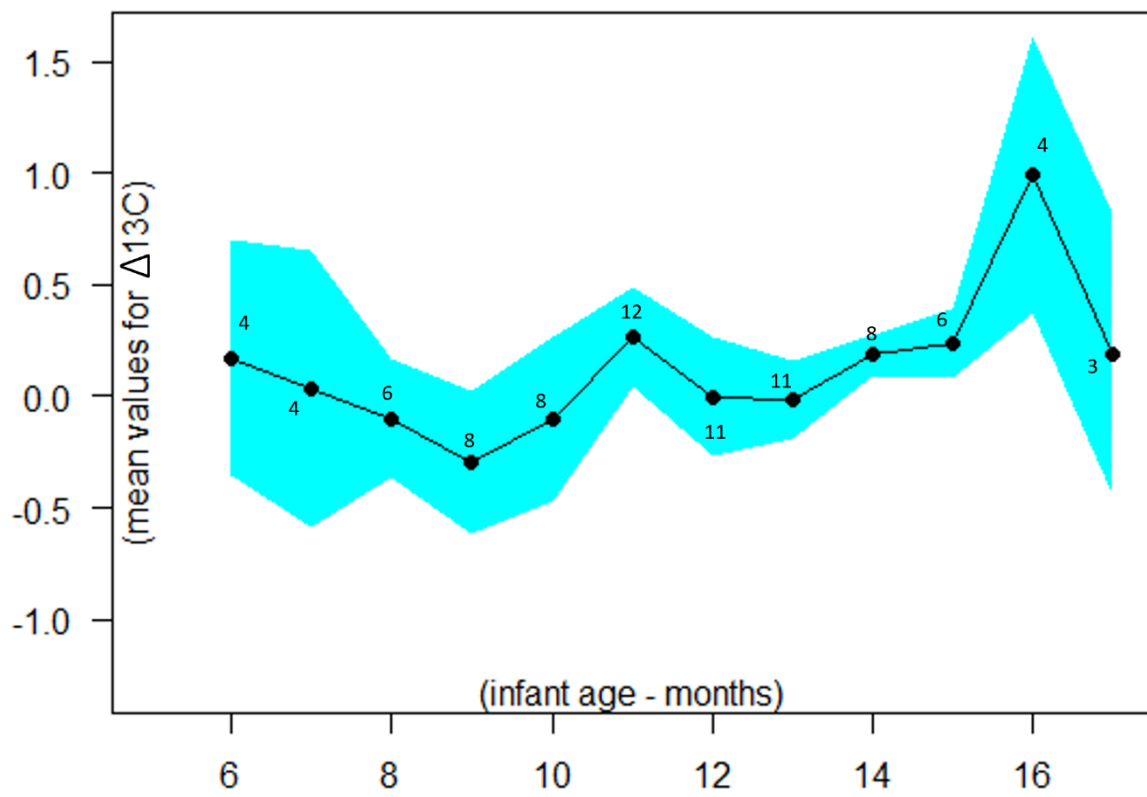
776 **Table S4.** Results of the non-significant interactions tested in our models predicting $\Delta^{15}\text{N}$ values ($N=90$
777 samples from 22 infants for each measure).

<i>Response variable</i>	<i>Explanatory variable</i>	<i>Estimate</i>	<i>standard error</i>	<i>degree of freedom</i>	<i>T value</i>	<i>P-value</i>
$\Delta^{15}\text{N}$	Rank x Within-infant age effect	-0.167	0.105	66.008	-1.592	0.116
	Maternal age x Between-infant age effect	-0.007	0.016	12.962	-0.442	0.666
	Maternal age x Within-infant age effect	0.001	0.008	66.009	0.135	0.893
	Offspring sex: Male ^a x Between-infant age effect	0.043	0.124	12.995	0.347	0.735
	Offspring sex: Male ^a x Within-infant age effect	-0.031	0.059	66.009	-0.514	0.609

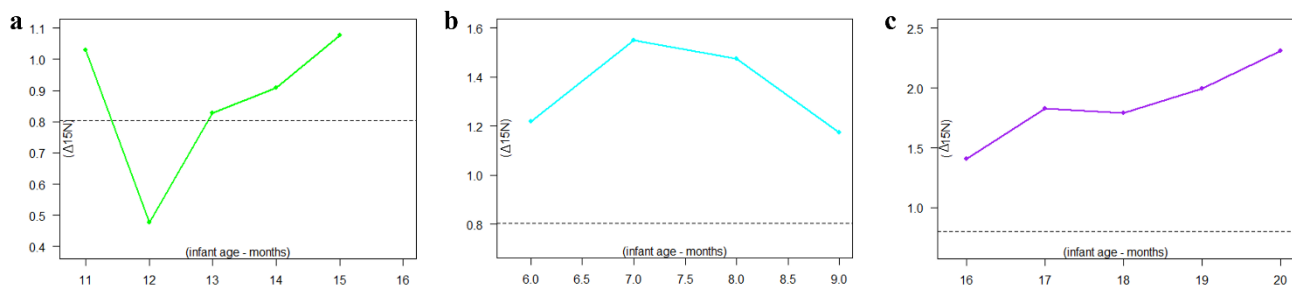
778 Reference category = ^aFemale

779 **Figure S1.** Variation with infant age in the mean difference between infant and mother $\delta^{13}\text{C}$ for each monthly
780 pair of samples (hair sections from mother and offspring). Standard errors are represented by a coloured area
781 around the main curve. The number near each dot indicates the number of mother-offspring pairs contributing
782 to each mean and standard error.

783



784 **Figure S2.** Example trajectories of $\Delta^{15}\text{N}$ values from three infants, compared to the between-mother standard
785 deviation for $\delta^{15}\text{N}$ (0.805) (dotted horizontal lines in the figures) to estimate the infants' weaning ages. We
786 were able to estimate weaning ages when $\Delta^{15}\text{N}$ values fell below the horizontal line. For example, the infant
787 illustrated in panel a weaned at 12 months of age (green), while the other two infants were too young (panel b,
788 in blue) or too old (panel c, in purple) for us to estimate the weaning age with these data. In fact, the main
789 difference between panel b and c (besides the age of the two infants) is that the high $\Delta^{15}\text{N}$ values in panel b
790 are probably due to consumption of milk whereas in panel c they are due to nutritional stress.



791 **Figure S3.** Age distribution (in months) of infants for whom we were able to estimate weaning age (green),
792 and those who we suspected had already weaned before the time period our hair samples covered (blue) or had
793 not yet weaned (purple). The mid-lines show the medians, the boxes the interquartile range, while the whiskers
794 show 1.5 times the interquartile range. Each dot represents a monthly sample.

